

the dorsal gland nucleus has retained its individuality. There is no evidence of atypical division such as nuclear budding, for the small nuclei are all of about equal size. The subventral esophageal gland orifices are near the anterior end of the esophagus while that of the dorsal gland is situated somewhat posterior.

*Leptosomatum* is provided with pigment spots or "ocelli" which are generally considered to be situated dorsal to the esophagus; the spots are acorn-

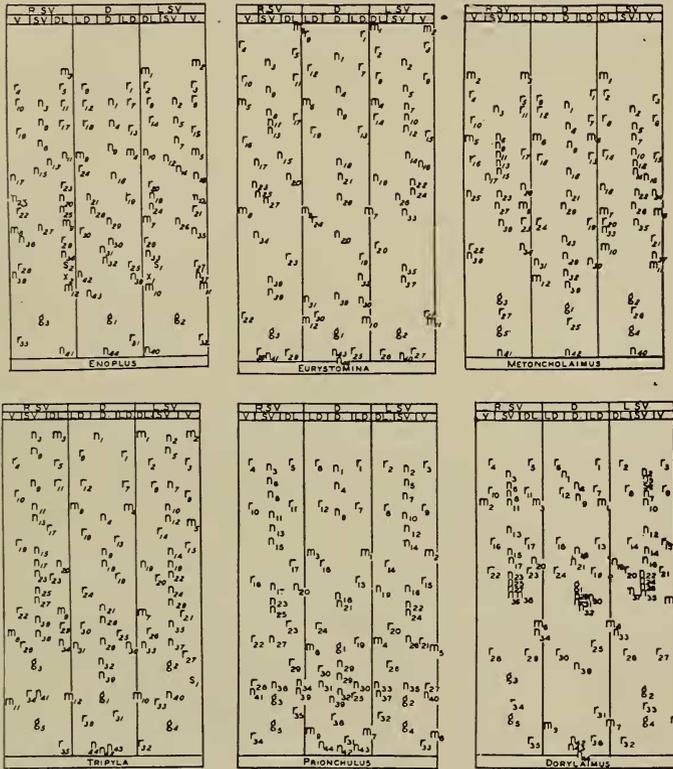


Fig. 2.—Tables of nuclear distribution in the Enoplida.

shaped and contain a distinct lens. Schulz (1931) described such ocelli in *Parasymphocostoma formosum*, stating that the lens is a continuation of the external cuticular covering of the body and that the presence of a special cell lying outside of the esophagus is responsible for this formation. In the present form, such is not the case. The pigment spot and lens form a swelling in the wall of the esophagus and are clearly of esophageal derivation. This is a peculiar situation in the origin of photoreceptors, if such they be, and supplies definite evidence of the homology of this type of ocellus with the pigment spots of forms such as *Enoplus*.

*Cryptonchus nudus* (Ironidae)

The esophagus of *Cryptonchus* grossly resembles that of *Dorylaimus* since it is clearly divisible into a narrow anterior muscular part and a wide pos-

terior glandular part. The long cylindrical stoma is surrounded by esophageal tissue throughout its length and the esophageal lining has marked attachment points for the concentrated radial muscles except in the basal region. The esophageal nuclei seem to follow the pattern seen in *Prionchulus* more closely than to any of the other enoplids, but the dorsal gland nucleus is situated near the level of  $g_{4-5}$  instead of being far anterior as in *Prionchulus* and *Dorylaimus*. Apparently the glands have orifices in the posterior part of the esophagus since no tubes extending anteriorly were observed. The rather thick esophago-intestinal valve is very well developed, triradiate, and consists of an anterior part which contains at least five nuclei of obvious esophageal origin followed by a posterior part (cardiac column) containing about 35 nuclei and apparently represents a differentiated region of the intestine.

*Ironella prismatolaima* (Ironidae)

The esophagus and stoma of *Ironella* are both cylindroid, the latter being surrounded by esophageal tissue and the stomatal region set off from the remainder of the esophagus as a distinct enlargement. The esophageal lining has large thickened attachment points for the radial muscles. The nuclear arrangement is apparently like that of *Cryptonchus*, and the 5 esophageal gland nuclei are subequal but the glands extend anteriorly through the stomatal region nearly to the base of the three bifurcate teeth.

*Ironus ignavus* (Ironidae)

This form appears to be somewhat intermediate between *Cryptonchus* and *Ironella*, having the gross morphology of *Cryptonchus* but the teeth of *Ironella*; the esophageal glands have orifices anterior to the base of the stomatal region, the subventrals opening near the teeth and the dorsal about midway between the teeth and base of the stoma.

*Phanodermopsis longisetae* (Enoplidae)

The general outline of the esophagus of *Phanodermopsis*, like that of *Eurystomina*, is of the type described as "conoid," but unlike the latter the margin of the posterior part of the esophagus is "crenate." The crenate appearance is due to development of the esophageal glands and reduction in the relative amount of muscular tissue, the strands of which are set off in relief causing the illusion of cells. The lumen is usually open toward the margins; the esophageal lining is simple.

The nuclear arrangement anterior to the nerve ring in this form appears to agree with that of *Enoplus*, except that the fourth group of radial nuclei is anterior to  $n_{12-13}$  instead of posterior to  $n_{26-27}$  as in *Enoplus*. Posterior to the nerve ring the number and distribution of nerve cell nuclei and marginal nuclei appear to be as in *Enoplus*, while there is a fifth group of 6 radial nuclei near the level of  $n_{37-38}$  (not far from the position of the fourth group of radial nuclei in *Enoplus*), and there appears to be 2 groups of 3 radial nuclei, or a complete sixth group, instead of 1 group of 3 radial nuclei (the diminished sixth group in *Enoplus*) near the posterior end of the esophagus. There are 2 extremely large subventral gland cell nuclei situated not far from the posterior end of the esophagus. Near the anterior end of the glandular region in the dorsal sector there are three bands of tissue each containing a nucleus; these probably are the dorsal and small subventral ( $g_{2-3}$ ) gland nuclei which in this case have moved to the dorsal sector.

The subventral esophageal glands extend to the anterior end of the

esophagus where they open directly into the lumen. The glandular tissue of the dorsal sector stains very intensely with hematoxylin, and near the level of  $m_{7-9}$  the tissue is distinctly subdivided into a dorsal and 2 subdorsal marginal lobes, each of which may represent a separate gland. While no orifice has been observed, it is certain that no glandular material extends anterior to  $n_{30}$  in the dorsal sector.

The esophago-intestinal valve is short, internally triradiate and externally circular, the whole containing 8 nuclei.

#### *Soboliphyme baturini* (Soboliphymatidae)

The esophagus of *Soboliphyme* is cylindrical and without subdivisions. Since there is no stoma, the anterior end of the esophagus projects slightly into the muscular oral sucker. The esophageal lumen is simple and triradiate throughout its length. The orifices of the three esophageal glands are situated at the extreme anterior end of the esophagus. From each of these orifices a short terminal cuticle-lined duct extends to a short distance posterior to the nerve ring where it bifurcates. Each branch is thick-walled and lined by a peculiar fibrillar layer which is apparently composed of "cilia." Still further posteriad the "cilia" disappear and the branches further subdivide until there may be as many as six parallel tubes in each sector of the esophagus. At times some of the tubules end blindly, while others divide. As a rule, the outer or most marginal tubules in each sector are the ones which terminate blindly while the others continue. There is little difference in the appearance of the glands except near the base of the esophagus. At this point the protoplasm of the dorsal gland tubules is reticulate and the lumen may contain a reticulated mass; the subventral gland tubules appear to have acidophilic granules imbedded in the tubule wall and the protoplasm is more dense than that of the dorsal gland tubes.

Exact information cannot be given regarding the nuclei of the esophagus since only one complete series of sections was available for study, and in places these sections may not have been correctly placed. However, the esophageal glands are multinucleate, each gland containing several hundred nuclei scattered throughout the length of the esophagus. The radial nuclei are in groups of 3, there being 2 groups anterior to the nerve ring and 5 or more groups posterior to that region. The marginal nuclei are likewise arranged in groups of 3. Between the second radial group and the first marginal group of nuclei 11 nerve cells were observed. The determination of other nuclei was difficult because of the great number of esophageal gland nuclei which obscured the picture. The esophago-intestinal valve is triradiate.

#### Other dioctophymatids

*Dioctophyma renale*, *Eustrongylides ignotus* and *E. perpapillatus*, none of which has an oral sucker, were all studied in comparison with *Soboliphyme*. The esophagus of *Dioctophyma* is similar to that of *Soboliphyme* except that no "cilia" were observed in the esophageal gland ducts. The dorsal gland ducts, after their primary bifurcation, were never seen to subdivide though every section in an incomplete series of 2000 sections was studied. The esophagi of *Eustrongylides ignotus* and *E. perpapillatus* were also studied in incomplete series, the findings agreeing with those in *Soboliphyme* except that no cilia or granules were observed in the gland tubules. The tubule branching occurs in all three glands and only the outer or marginal tubules in each sector terminate blindly. Slides of these forms always show a marked

differential staining of the glands, the dorsal being acidophilic and the subventrals basophilic. This is particularly marked when stained in a Mallory triple stain, the subventrals being orange or red, the dorsal blue. Subventral gland tubules entering the dorsal sector were only observed in *Diectophyma* but whether or not this occurs in *Soboliphyme* or *Eustrongylides* is not known; no such case has been observed.

Unfortunately our observations of the esophagi of this particular group, the Diectophymatina, are not so complete as might be desired. Nevertheless it does serve further to indicate the possible relationships of the forms. In this connection, it may be noted that the dorsolateral mesenteries of the intestinal region begin anteriorly as a single ventral mesentery from the esophagus, which splits before reaching the body wall subventrally. Gradually as one traces the mesentery posteriad the split becomes wider, the single mesentery ultimately forming two subventral mesenteries, two ventrolateral, two lateral, and finally, two subdorsal.

#### *Dorylaimus obtusicaudatus* (Dorylaimidae)

The esophagus of this species consists of a short narrow anterior muscular part and a long wide posterior glandular part. There is no distinct stoma in the sense that this structure is present in *Prionchulus*, it having been replaced by a well developed stylet. The stylet is joined at its base with the cuticular lining of the anterior end of the esophagus. The lumen of the esophagus is at first open, wide, and subtriangular (see Chitwood, 1931, fig. 22, No. 5), gradually becoming smaller, the esophageal lining thicker (Chitwood, loc. cit. Nos. 6-7) and with radial thickenings similar to those present in *Prionchulus*. These thickenings are largest in the posterior part of the narrow muscular region but continue throughout the remainder of the esophagus.

There are 36 radial muscle nuclei arranged in 6 groups as in *Prionchulus*; there are 9 marginal nuclei, also arranged as in *Prionchulus*; comparison with the latter form indicates that in *Dorylaimus*  $n_{23}$ ,  $n_{30}$ , and  $n_{41}$  are absent, but it may be that they are merely obscured by glandular tissue. It may also be noted that the group  $n_{29-32}$  is more compact than in other forms. A nucleus (st) not present in other forms, is characteristic of the Dorylaimidae. This nucleus, situated in the anterior muscular part of the esophagus is that of the formative or generative cell of the stylet.

Four well developed esophageal gland nuclei, 1 in the dorsal sector ( $g_1$ ), 2 in the left subventral sector ( $g_2$  and  $g_4$ ) and 1 in the right subventral sector ( $g_5$ ), are present. The other esophageal gland nucleus ( $g_3$ ) is much smaller than the former and easily overlooked. The dorsal gland nucleus lies relatively much farther forward than in *Prionchulus*. Each gland has a separate orifice situated near the level of its nucleus. The dorsal gland is very much lobed and branches of it enter into all sectors of the esophagus. The subventral glands, on the contrary, remain within their sectors and their tubules are relatively smaller.

The esophago-intestinal valve is elongate, dorso-ventrally flattened and contains about 27 nuclei.

#### Other dorylaimoids

The esophagi of such forms as *Actinolaimus*, *Leptonchus* and other close relatives of *Dorylaimus* appear to be histologically identical to that of the latter form, while that of *Triplonchium* differs considerably. The short bulbar region in *Triplonchium* is literally packed with nuclei, presumably be-

cause all of the nuclei of the more elongated glandular region of *Dorylaimus* are concentrated in less space. The dorsal gland nucleus and those of the first pair of subventrals are subequal in size and smaller than those of the second pair of subventrals. The esophageal lining appears to be simple, unmodified, but this may be due to its extreme minuteness.

*Agamermis decaudata* (Mermithidae)

The esophagus of *Agamermis decaudata* undergoes considerable transformation during its development. In order to understand satisfactorily the esophagus of the later parasitic stages and adults a brief résumé of the earlier stages is necessary.

Christie (1936) described the morphology of the various larval stages of *A. decaudata* and the essentials of this description are as follows: In the pre-parasitic larva the digestive tract consists of a stylet followed by the esophagus and intestine. The anterior part of the esophagus is narrow, muscular, surrounded near the middle of its length by the nerve ring; the narrow anterior part is followed by a short elongated muscular swelling posterior to which there is a long glandular region. In the latter region the esophagus proper is very narrow and surrounding it are three large elongated esophageal glands and 2 rows of 8 smaller cells, the stichocytes. The largest gland is unicellular, right subdorsal in position, and extends from the esophageal swelling to the base of the esophagus; the two unicellular subventral esophageal glands are left subventral in position and extend posteriorly from the esophageal swelling to about  $\frac{1}{4}$  the length of the glandular part of the esophagus; the stichocytes extend from slightly anterior to the base of the subventral glands to the posterior end of the esophagus. At this time the intestine does not extend anterior to the base of the esophagus.

Shortly after entrance into the host the three esophageal glands become atrophied while the stichocytes become larger and the intestine begins growing anterior to the base of the esophagus.

The present study was based on partially grown parasitic larvae about 5 mm long (approximately 1 to 2 days in host) at which stage the external cuticle is still thin, though otherwise the larvae is in much the same condition as it is at the time of its emergence from the host.

At this stage the esophagus is no longer distinctly muscular in any region, the elongated swelling posterior to the nerve ring has disappeared, and the trophosome extends anteriorly nearly to the level of the anterior esophageal glands. The stichocytes are large, forming a double row of elongated cells with their ends touching one another.

Anterior to the nerve ring the lumen is internally hexagonal, the lining thick and externally rounded to subtriangular in cross section. There is a group of 9 small nuclei near the oral opening, which appear to be radial or marginal in character. The surrounding esophageal tissue is spongy, without apparent symmetry. Posterior to these nuclei, there are 12 large rather irregularly arranged nuclei ( $r_{1-12}$ ) anterior to the nerve ring. Between the nerve ring and the orifice of the dorsal esophageal gland the esophageal nuclei, lining, and general structure are like that part anterior to the nerve ring. In this region 15 large nuclei ( $r_{13-37}$ ) and at least 5 nerve cell nuclei ( $n_{1-5}$ ) are present. The region of the esophageal glands contains 4 nerve cells ( $n_{6-9}$ ) and 3 large nuclei ( $r_{23-30}$ ) in addition to the 3 gland nuclei ( $g_{1-3}$ ). Each gland has at least 1 distinct orifice, sometimes several.

Posterior to the gland nuclei ( $g_{1-3}$ ), the chief part of the esophageal tissue containing the esophageal lumen is flattened between the two large rows of